

Hydrographic features and seabird foraging in Aleutian Passes

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Running title: Hydrographic features and seabird foraging

ABSTRACT

Strong tidal currents crossing over the abrupt topography of the Aleutian Passes result in regions with high horizontal property gradients. These frontal regions vary with the tidal cycle and form the boundary between vertically mixed and stratified regions. Concentrations of seabirds were associated with convergence zones in the mixed water and with the front between North Pacific water and mixed water. Species that were foraging by picking at prey from the surface were associated with surface convergences that appeared to be associated with Langmuir circulation cells or tidal features (all fulmar aggregations) in the central passes (Samalga, Seguam). In contrast, subsurface foraging puffins and small alcids were mostly observed in areas of turbulent, well-mixed water near the shallow regions of the passes. Short-tailed shearwater flocks that were plunge-diving for prey were associated with the front between the North Pacific and mixed waters in the passes. On our transects, we observed no significant aggregations of seabirds associated with Bering Sea water or North Pacific water away from the frontal zones. The interaction of strong currents with bathymetric features results in zones of vertical advection, mixing, and surface convergences that make island passes attractive foraging regions for seabirds. Deep passes lacking these features, such as many of the passes in the western Aleutian Archipelago, are not as likely to facilitate trophic transfer to top predators as shallow passes, such as those found in the eastern Aleutian Islands.

KEY WORDS: Aleutian Islands, Aleutian Passes, convergences, *Fulmarus glacialis*, northern fulmar, *Puffinus tenuirostris*, seabird foraging, short-tailed shearwater, tidal fronts, trophic transfer, zooplankton.

INTRODUCTION

The Aleutian Archipelago comprises the boundary between the North Pacific Ocean and the Bering Sea. This region supports an extremely rich ecosystem including many varieties of fish, marine mammals, and seabirds. The oceanography in the Aleutian passes is highly dynamic, with intense tidal oscillations superimposed on highly variable lower frequency currents (Stabeno *et al.*, 2005). The combination of strong, variable currents, abrupt topography, and distinct water masses from two separate ocean basins results in numerous fronts separating mixed and stratified regions.

The physical features inherent in such a dynamic environment (fronts, eddies, tidal rips, etc.) influence seabird prey distributions (e.g. Hunt *et al.*, 1998; Hunt *et al.*, 1999). Their zooplankton prey can be concentrated either in the vertical (at the pycnocline in stratified water; Cooney, 1989; Fragopoulou and Lykakis, 1990; Hunt *et al.*, 1990), or as horizontal patches (Hunt *et al.*, 1998). Surface convergences concentrate floating or weakly swimming organisms at the surface (Franks, 1992), and tidal currents interacting with bathymetry result in the upwelling of zooplankton near the bottom (Wolanski and Hamner, 1988). Vertically migrating zooplankton can become concentrated when they swim against currents (Coyle *et al.*, 1992; Simard *et al.*, 1986). Or, prey may be advected into shallower regions to become trapped against the bottom (Genin *et al.*, 1988; Hunt *et al.*, 1996).

Considerable variation in the abundance and species composition of seabirds has been observed in the Aleutian passes (Jahncke *et al.*, 2005), and seabird distribution within the passes is patchy. The eastern passes (Unimak, Akutan and Umnak) are narrower and shallower than the central passes (Samalga, Seguam and Tanaga) (Ladd *et*

al., 2005). In addition, the eastern and central passes have been shown to have different water properties (eastern: coastal; central: oceanic; Ladd *et al.*, 2005), zooplankton species composition (eastern: neritic; central: oceanic; Coyle, 2005), and seabird species composition and diet (eastern: dominated by shearwaters; central: dominated by fulmars; Jahncke *et al.*, 2005).

In this study, we investigated the hydrographic structure of the water masses and frontal features within the eastern and central Aleutian passes, with focus on Unimak, Akutan, Seguam, and Tanaga Passes (Fig. 1). We examined the relationships between physical features and the distribution of aggregations of foraging seabirds. Our analyses focused on the most abundant seabird species that exhibited significant foraging aggregations: short-tailed shearwater (*Puffinus tenuirostris*), northern fulmar (*Fulmarus glacialis*), ancient murrelets (*Synthliboramphus antiquum*), Least auklets (*Aethia pusilla*), whiskered auklets (*Aethia pygmaea*), and tufted puffins (*Fratercula cirrhata*).

METHODS

The eastern and central Aleutian Passes were visited in May and June of 2001 and 2002 (Fig. 1; Table 1). On multiple transects through the passes we recorded hydrographic structure (salinity and temperature), zooplankton distributions (MOCNESS and CalVET net tows and acoustics), and seabird distributions (systematic seabird surveys).

CTD (conductivity, temperature, and depth) casts were taken with a Sea-Bird SBE-911 Plus system. Salinity calibration samples were taken on all casts and analyzed on a laboratory salinometer. Underway surface temperature and salinity were collected with a Sea-Bird Electronics thermosalinograph installed in the ship's seachest. Note that a full transect takes $\sim 7 - 12$ hours and therefore, observations at one end of the transect are taken on a different tidal phase than those at the other end of the transect. The direction of the tides influences the position of the observed fronts. Tidal phase and time of change on each transect is noted in Table 1. For details on physical measurements, their calibration and analysis, see Ladd *et al.* (2005).

Acoustic data were collected using a Hydroacoustic Technology Inc. (HTI) model 244 split-beam digital system. During 2001, the acoustic data were collected with four transducers: a 420 kHz 6° single beam, and 43 kHz 7°, 120 kHz 6° and 200 kHz 3° split-beam transducers. During 2002, the data were collected with 420 kHz 3°, 120 kHz 6°, and 200 kHz 3° split-beam transducers. The transducers were towed beside the vessel at about 3 m s^{-1} in a dead-weight tow body about 4 m from the hull and 2 m below the surface. Acoustic transects were run through the passes during the day in the direction of current flow. The system collected 20 log R data for echo integration using 15 s time intervals and 1 m depth intervals resulting in a sample interval of about 45 m. The

acoustic data were converted from volume scattering to estimates of acoustically determined zooplankton biomass (ADB) by direct comparison of net data as discussed by Coyle (2005).

Interpretation of acoustic data is complicated by the fact that the density of sound scattering organisms is a function of both the time of day that the acoustics were collected and the water column properties. The data from Unimak Pass for example (not shown), show high concentrations of zooplankton on the north side of the pass because the data were collected when it was starting to get dark. In addition, acoustic determination of biomass in convergence zones is confounded by the entrainment of bubbles, which scatter sound and produce artifact in the data. Some of this artifact was observed in Akutan Pass, where flow through the pass was sufficient to generate this artifact. It is therefore necessary to eliminate data from strong convergence zones to avoid misinterpretation of the results. Because of the above complications, simple correlations between seabird concentrations and acoustically determined biomass will not necessarily be observed.

Data on the distribution and abundance of seabirds were obtained by counting seabirds from the bridge of the R/V *Alpha Helix* (eye height = 7.7 m above the sea surface) while the ship was underway. Vessel speed varied from 11 km h⁻¹ to 19 km h⁻¹ depending on whether we were conducting acoustic or CTD surveys. Birds were counted continuously during daylight hours in a 300 m arc from directly ahead of the vessel to 90° off the side with best visibility (i.e. lowest glare) and were logged into a portable computer. Observers switched to a snapshot method of counting when large aggregations of birds (> 1,000 individuals) were encountered crossing the bow of the vessel (Tasker *et*

al., 1984). Seabird behaviors were recorded as flying, sitting on the water, and feeding. Seabirds sitting on the water were assumed to be about to forage, or to be resting from a previous foraging bout.

We divided the transects through the passes into non-overlapping regions based on hydrographic features such as stratification and frontal structures. In the majority of transects, surface density exhibited three regions with fairly constant surface density separated by two fronts (regions of high horizontal gradients in surface density). We called the northernmost water mass Bering Sea (BS) water, the water mass in the center of the pass mixed water (MW), and the southern water mass North Pacific (NP) water. The NP water is derived from Alaska Coastal Current water in the eastern passes (Unimak, Akutan, Umnak and Samalga) and Alaskan Stream water in the central passes (Seguam and Tanaga) (Ladd *et al.*, 2005). The front separating the BS water from the MW is called the BS/MW front, while the front separating the MW from the NP water is called the NP/MW front. The locations of the frontal regions were calculated as the locations of high horizontal gradient in surface density from the underway system. Where the frontal regions were not well defined, we note that information in the tables (Tables 2 – 5). The width of the frontal regions was extended 1 km to the north and south of each front to include seabirds foraging in the vicinity of the front.

We used the utilization test to examine the significance of seabird use of the different water masses and frontal features (Haney and Solow, 1992). Assuming a uniform distribution of seabirds along each transect, we calculated an expected value for the number of seabirds that should have occurred within each water mass and frontal area. This expected value is based on the total number of seabirds counted along the

transect and the amount of survey effort (km surveyed) spent in each area. Observed values were compared to expected values and 95 % confidence intervals were constructed according to the methods of Neu *et al.* (1974) for the observed proportions of birds for a Type I error rate of ± 0.05 . We conducted the analyses separately on each transect surveyed.

We used permutation analysis (Riehle *et al.*, 2001) to determine the location of significant aggregations of seabirds along transects where no clear water masses were identified. We determined the observed density of birds based on a 5 km (50 100-m bins) sliding window that moved through the series of data. The expected density of birds and the confidence intervals were obtained by using a permutation testing procedure. The mean, variance and 95% confidence intervals in density of birds were calculated over 500 random permutations of the order of 500 100-m bins sampled from the remaining length of the transect. Bird aggregations were considered significantly higher when densities within the sliding window were larger than the 95% confidence interval estimated for the remainder of the transect.

RESULTS

Shallow, eastern passes (< 100 m deep)

Unimak Pass

Unimak Pass is the first pass encountered by the Alaska Coastal Current as it flows westward along the shelf of the North Pacific. The shallowest part of the pass is less than 80 m deep and, at its narrowest, it is approximately 20 km wide. On the North Pacific side of Unimak Pass, the shelf is wide and our surveys did not reach the shelf break. On the Bering Sea side of the pass, the depth drops dramatically from ~100 m within the pass to greater than 400 m in less than 10 km (Fig. 2). Six transects through Unimak Pass were sampled (2 in 2001; 4 in 2002) with 3 CTD and 3 acoustic transects (Table 1). The longest transect surveyed in Unimak Pass was approximately 125 km.

North Pacific (NP) water, with its warm, low-salinity, low-density signature, was observed on the south side of Unimak Pass while cooler, saltier, denser Bering Sea (BS) water was observed at the north end of the pass (see Fig. 2 for an example transect). Due to its low density, the NP water intruded into the pass in the top 20 – 40 m overlying a strong pycnocline. A region of reduced stratification (mixed water; MW) was often observed near the shallowest part of Unimak Pass. Surface density in the center of the pass was generally higher than the NP surface water and lower than the surface BS water (Fig. 2d). That density structure, along with temperature and salinity properties, suggests that the water in the middle of Unimak Pass was primarily a result of lateral mixing between shallow NP and BS waters (Ladd *et al.*, 2005).

Surface density in Unimak Pass often exhibited sharp horizontal gradients (fronts) that were usually apparent in both temperature and salinity. Occasionally, however, fronts were only apparent in the surface salinity, while the surface temperature exhibited no strong gradient. The strength and position of the surface expression of the fronts, and the width of the frontal regions varied in time. The fronts sometimes represented the boundaries between two of the three water masses (NP, MW, and BS), but the fronts may have also indicated transient eddies and/or other features. Multiple surface density fronts in Unimak Pass may have been the result of pulses of NP water advecting through the pass on different phases of the tides. These pulses were often too small to be resolved by the CTD station spacing, but were apparent in the surface temperature and salinity measured by the underway system. In Unimak Pass, the NP/MW front was usually stronger and narrower than the BS/MW front.

In Unimak Pass, foraging and sitting shearwaters were significantly concentrated (Utilization test, $p < 0.05$) in the vicinity of the NP/MW front (Table 2). Approximately 1400 shearwaters were found aggregated just on the mixed-water side of the NP/MW front on 18 June 2001 (UN0101; Fig. 2; Table 2). This location also coincided with the shallowest point in the transect. South of the front, the water column was stratified with a warmer, fresher ($> 7.5\text{ }^{\circ}\text{C}$; $< 31.7\text{ psu}$) surface layer approximately 20 m deep (Figs 2f and 2g). Surface density in this stratified region exhibited two additional fronts that may have indicated a small ($< 10\text{ km}$ diameter) cyclonic eddy (Fig. 2d). No shearwaters were associated with this feature (Fig. 2a). In the mixed water region, temperature and salinity were well mixed to the bottom (5.7°C , 32.0 psu , 64 m depth).

On another occasion, an aggregation of approximately 375 shearwaters was observed sitting on the water just on the mixed-water side of the NP/MW front (UN0203; Table 2). Six hours later, on a second transect through Unimak Pass (UN0204), an aggregation of approximately 55 shearwaters was observed sitting on the water over the NP/MW front that was approximately 3 km north of its previous location. The northward shift in the location of the front was due to the direction of the tidal currents changing from southward flowing during our observation of the NP/MW frontal region of the first transect to northward flowing during the second.

On 20 May 2002, a significant aggregation (Permutation analysis, $p < 0.05$) of shearwaters (ca. 230 birds) was found at the northern end of the transect (UN0201; Table 2). The location of the birds coincided with the highest fluorescence in the transect, which may have attracted grazing euphausiids, a principal prey of the shearwaters in this area (Jahncke *et al.*, 2005).

Two species of pursuit diving seabirds, ancient murrelets and tufted puffins, showed significant aggregations over the MW of Unimak Pass (Tables 2 and 3). Feeding and sitting ancient murrelets were significantly aggregated over the MW in 2002 (UN0202: 54 birds, Table 3), as were tufted puffins (Utilization test, $p < 0.05$, Table 4) in 2001 and 2002. An exception to this pattern was observed in 2001 (UN0101), when tufted puffins were concentrated (ca. 53 birds) at the NP/MW front (Table 4).

Akutan Pass

Akutan Pass is approximately 60 m deep at its shallowest, slightly shallower than Unimak Pass. It is also about half as wide (~10 km) as Unimak. On the Bering Sea side of the pass, the depth drops to greater than 800 m in less than 10 km, even more

dramatically than in Unimak Pass. Three transects were sampled in 2001 (2 CTD and 1 acoustic transect) and five in 2002 (2 CTD and 3 acoustic transects) (Table 1). Two of the transects (AK0206 and AK0207) were aborted before obtaining a full transect through the pass.

In all six full transects, a surface density front (with decreasing density to the south) was apparent in Akutan Pass south of 54° N (see Fig. 3d for example). This front defined the northern edge of the NP water. The mixed region in the center of the pass was larger and more consistent ($25.4 < \sigma_t < 25.6$) than in Unimak Pass and was separated from the NP waters by well-defined surface density fronts. The division between MW and BS water was illustrated by increasing stratification in the northern part of Akutan Pass. The BS/MW front and the MW/NP front both slant toward the south with depth with deep BS water underneath MW and MW underneath NP water (Fig. 3). As in Unimak Pass, the temperature, salinity, and density suggest that Akutan Pass MW is a lateral mixture of shallow BS and NP waters.

In Akutan Pass on 14 June 2001 (AK0103), we encountered ~ 9,500 shearwaters (ca. 20,000 total birds in flock including birds foraging beyond the 300 m limit) feeding and sitting on the water along the NP/MW front at the southern end of the pass (Utilization test, $p < 0.05$; Fig. 3; Table 2). The northern edge of the aggregation coincided with the location of the greatest horizontal gradient in temperature and salinity. The largest part of the aggregation was over the more stratified NP water. When we returned later that day with an acoustic survey, we found about 40 shearwaters in about the same region (south of the NP/MW front), but no evidence of euphausiids in the upper water column (Fig. 4). A day later (AK0105; Table 2), approximately 3,700 shearwaters

(ca. 10,000 total birds in the flock including birds foraging beyond the 300 m limit) were associated with the NP/MW front, but just on the mixed-water side of the front. On both days, shearwaters were actively feeding on euphausiids (primarily *Thysanoessa inermis*), as evidenced by the prey regurgitated by birds leaving the area and prey found in the stomachs of shot birds (Jahncke *et al.*, 2005).

No shearwaters were observed foraging in Akutan Pass in May (3 transects) or June (2 transects) 2002. We do not know why foraging shearwaters were absent from our transects in this pass in 2002, but dense aggregations of birds (5,000 to 20,000 birds km⁻²) sitting on the water were found covering the water to the horizon in all directions north and west of Unimak Pass in June 2002 (Jahncke, unpublished data). It may be that shearwaters foraging in the vicinity of Akutan and Unimak passes move between the passes and adjacent shelf areas depending on the availability of near-surface aggregations of euphausiids. Based on many past visits to the region, there are almost always large flocks of foraging shearwaters present, but their exact location with respect to the two passes is highly variable and their use of frontal regions may in part reflect their use of sub-adult euphausiids (Vlietstra *et al.*, 2005; G.L. Hunt, personal observations).

Three species of pursuit-diving seabirds, ancient murrelets, whiskered auklets, and tufted puffins, were found foraging in significant aggregations in Akutan Pass (Tables 3 and 4). Ancient murrelets aggregated over the MW region in 2001 (AK0103: 71 birds, Table 3), as did whiskered auklets in 2001 (AK0103: 1110 birds; AK0104: 169 birds). Similarly, we found significantly more tufted puffins than expected by chance (Utilization test, $p < 0.05$, Table 4) feeding and sitting on the water over the MW region of Akutan Pass in both 2001 and 2002.

Umnak Pass

Umnak Pass is shallow (~ 25 m at its shallowest) and narrow (~ 5 km wide). Umnak was sampled on two transects, both in 2002. Surface waters were colder and saltier at the north end than at the south end of the pass during both sections. However, the three water masses and accompanying fronts exhibited by other passes were not so apparent in Umnak. Instead, the mixed region in the center of the pass exhibited many small-scale surface fronts and it was difficult to distinguish three distinct water masses.

We found significant aggregations (Permutation analysis, $p < 0.05$) of ancient murrelets (UM0210: 134 birds; UM0211: 143 birds; Table 3) and tufted puffins (UM0210: 290 birds; UM0211: 190 birds; Table 4) feeding and sitting on the water over the central and northern regions of Umnak Pass in 2002. CTD data for this pass showed no clear water masses; however, our observations suggest that the ancient murrelets were associated with tide rips and convergences. The tufted puffins in this pass were foraging over an area of strong tide rips during our first survey, and were foraging north of the strongest tide rip, likely associated with a strong convergence, during our second survey of the pass.

Central passes of intermediate depth (100–500 m deep)

Samalga Pass

Samalga Pass (depth ~ 200 m; width ~ 29 km) marks a transition between the eastern passes which are dominated by Alaska Coastal Current (ACC) water and a neritic or shelf ecosystem, and the central passes which are dominated by Alaskan Stream water and an oceanic ecosystem (Coyle, 2005; Ladd *et al.*, 2005). Our CTD survey of the length of

Samalga Pass was disrupted by bad weather and thus our physical description of this pass is incomplete. Nevertheless, water throughout the pass was fairly well stratified, though there was evidence of strong vertical displacements in the isopycnals (Ladd *et al.*, 2005). A transverse CTD line showed that the eastern side of the pass was dominated by relatively fresh water of ACC origin whereas the western side of the pass was dominated by saltier Alaskan Stream and/or BS Water.

In Samalga Pass, we found significant aggregations (Permutation analysis, $p < 0.05$) of northern fulmars in 2002 (SA0212: 334 birds; SA0213: 1,572 birds; Table 5) near the middle of the transects. On 7 June (SA0212), fulmars in this area were lined up on what appeared to be Langmuir cells, and on 8 June (SA0213) they were foraging in tight flocks over slicks associated with convergences.

Seguam Pass

Seguam Pass is deeper and wider than the eastern passes (35 km wide, 100 m deep). The minimum depth in Seguam Pass is approximately 100 m with an average depth of ~150 m over the ~50 km long pass. The shallowest part of the pass is only ~20 – 30 km long. Four transects through Seguam Pass were sampled (1 CTD and 1 acoustic transect in each year). Each of the transects exhibited well-defined surface density fronts separating the MW in the center of the pass from the NP water in the south and the BS water in the north (Fig. 5). The MW was denser than either the BS surface water or the NP surface water reflecting the influence of deeper water mixed to the surface (vertical mixing as opposed to the lateral mixing that dominates in the eastern passes; Ladd *et al.*, 2005). This vertical mixing is due to a combination of factors including the shorter along-pass distance and higher current speeds in Seguam relative to the eastern passes (Stabeno *et*

al., 2005). Salinity levels in the mixed water of the central passes were much higher than in the eastern passes, reflecting the influence of both vertical mixing and the higher salinity of the source waters (Alaskan Stream as opposed to ACC). The position of the fronts appears to be tied to the topographic break at either end of the pass with the surface expression of the front advected north or south of the topographic break depending on the phase of the tide. This frontal structure is particularly apparent in the relatively simple geometry of Seguam Pass (Fig. 6).

In Seguam Pass, significantly more shearwaters than expected by chance (Utilization test, $p < 0.05$) were found feeding and sitting on the water over the MW at the middle of the pass in 2002 (Utilization test, $p < 0.05$, Table 2). Approximately 72 birds were observed feeding in tight groups over slicks or loosely spread out over frontal structures (SG0218; Fig. 7). Although the cause of these slicks was not resolved by either the CTD transects or the continuous underway sea surface property measurements, observations from the ship's bridge suggest that these slicks were related to convergence zones and tidally-driven eddies. Convergence is also suggested by the large biomass of copepods and euphausiids distributed vertically to almost 100-m depth. The largest aggregation of shearwaters was co-located with this vertical distribution of biomass (Fig. 7). The shearwaters were actively foraging on euphausiids (primarily *Thysanoessa longipes*) as evidenced by regurgitates and stomach analysis (Jahncke *et al.*, 2005).

Approximately 650 fulmars were observed foraging in scattered groups over areas of slick water on 10 June 2001 (SG0107: Table 5). The majority of these were observed over the northern end of the MW region, south of the BS/MW front. A day later (SG0108), we found approximately 500 birds scattered along slicks parallel to the ship's

course; the distribution had shifted approximately 15 km south along with the BS/MW front. Both transects were taken on the ebb (southward) flowing tide. Fulmars on June 11 (SG0108) were distributed over the entire mixed water region with very few birds observed north of the BS/MW front or south of the NP/MW front. An aggregation of approximately 350 fulmars were observed sitting on the water over ~ 7 km region just south of the BS/MW front in June 2002 (SG0217; Table 5). One day later (SG0218), approximately 1,865 fulmars were observed actively feeding in lines together with shearwaters over slick areas parallel to the wind, possibly the result of Langmuir circulation cells. Birds over the slick areas were in tight lines or groups pecking at the surface. Birds over fronts were loosely spread out (Fig. 7). The northern edge of the distribution was just north of the BS/MW front, with the majority of the birds observed over the mixed water south of the front. The aggregation did not reach as far south as the NP/MW front.

In both 2001 and 2002 at Seguam Pass, we found foraging and sitting tufted puffins concentrated on the water over the MW region (Utilization test, $p < 0.05$; Table 4).

Tanaga Pass

The minimum depth in Tanaga Pass is approximately 160 m with an average depth of ~350 m over the approximately 20 km-long pass. One CTD transect and one acoustic transect were sampled in Tanaga Pass in late May 2002 (Table 1). As in Seguam Pass, the MW in Tanaga is denser and higher in salinity than the surface waters to either the north or the south (Fig. 8), reflecting the influence of deeper water mixed to the surface.

Least auklets (*Aethia pusilla*), feeding and sitting on the water, were significantly more abundant than expected by chance over the MW region in Tanaga Pass in 2002 (TN0219: 9,242 birds; TN0220: 1,401 birds, Table 3; Fig 8). The aggregation of actively foraging least auklets occurred in an area of boils and convergences resulting from the interaction between a northward tidal flow and the shallow bathymetry of a submerged mountain (51.6° N, 178.2° W, 80 m deep; not seen in Fig. 8, but recorded by the ship's depth sounder). Our observations suggest zooplankton was physically forced to the surface and aggregated in this area as evidenced by the copepod prey (*Neocalanus plumchrus-flemmingeri*) found in the stomachs of shot birds (Jahncke *et al.*, 2005).

DISCUSSION

North Pacific (NP) water, with its warm, low-salinity, low-density signature, was observed on the south side of the passes. In each pass, a front separates the North Pacific water from the mixed water (MW) observed in the center of the pass. A second front separates the MW from the Bering Sea (BS) water at the north end of the pass (Fig. 9). Note that the schematic showing three water types in Fig. 9 is simplistic. In reality, there are often numerous fronts of varying strength (as opposed to the two shown in the schematic).

Eastern vs. Central Passes

Generally, in the eastern passes, the surface density of the BS surface water is denser than the MW, which in turn is denser than the NP surface water (Fig. 9). Comparing temperature and salinity properties of the three water types shows that, in the eastern passes, the MW is formed via (primarily lateral) mixing between shallow NP and BS waters. The northern front (separating BS water from MW) often appears to tilt to the south with depth such that the BS water undercuts the MW. The movement of BS water into the pass at depth may be dependent on the phase of the tidal cycle, with denser BS water observed at depth in the passes most frequently on the ebb (southward flowing) tide.

The central passes are generally shorter, deeper, and wider than the eastern passes. This topography allows for higher current speeds and larger transports (Stabeno *et al.*, 2005). The sill depth in Seguam Pass (Tanaga Pass) is approximately 100 m (160 m) with an average depth of ~150 m (350 m) over the ~50 km (20 km) long pass. In

Seguam and Tanaga Passes, the MW is denser than either the BS surface water or the NP surface water reflecting the influence of deeper water mixed to the surface (vertical mixing as opposed to the lateral mixing that dominates in the eastern passes).

Marine bird uses of the passes

In the shallow eastern passes (Unimak, Akutan and Umnak), short-tailed shearwaters and tufted puffins were most common (Jahncke *et al.*, 2005). In Samalga and Seguam, central Aleutian Archipelago Passes, northern fulmars were most common although shearwaters were also observed (Jahncke *et al.*, 2005). Least auklets were the most common seabird observed in Tanaga Pass (Table 1).

Although most (21 of 28) transects through the passes encountered at least 50 individuals of one of the six seabird species on which we focused, any one species was present in numbers ≥ 50 on a minority of the transects through the eastern and central passes. Short-tailed shearwaters were present in numbers ≥ 50 on 7 of 28 transects, northern fulmars on 6/28 transects, tufted puffins on 13/28 transects, and three species of small alcids combined on 10/28 transects. One reason that a given species was abundant on a small proportion of the transects was a result of the large-scale distribution of species; shearwaters were present in large numbers in only three of six passes (Unimak, Akutan and Seguam), fulmars were present in only two (Samalga and Seguam), and tufted puffins were numerous in four passes (Unimak, Akutan, Umnak and Seguam) (Jahncke *et al.*, 2005). Of the small alcids, ancient murrelets had significant aggregations in three passes (Unimak, Akutan and Umnak), Whiskered auklets had aggregations in one pass (Akutan), and least auklets had significant aggregations only in Tanaga Pass. In the central passes (Seguam and Tanaga), only the least auklet had significant aggregations,

although small numbers of small alcids were also present in Seguam Pass. Amukta Pass, a wide (68 km), deep (430 m) central pass, had no significant seabird aggregations on three separate transects (1 in 2001; 2 in 2002).

There was considerable variation in the distribution of seabird aggregations between visits to passes within a year, and from one year to another. Part of this variation was undoubtedly related to the phase of the tide during our transects, but other factors, such as seasonal differences and patchiness in the availability of zooplankton (Coyle, 2005) must have been important as well.

Within these passes, if ≥ 50 birds of a species were present, then they were likely to be in statistically significant aggregations: 7 significant aggregations of shearwaters were observed within 7 transects, 9/6 for fulmars, 12/13 for tufted puffins, and 8/10 for small alcids. These aggregations were not evenly distributed among the water masses and hydrographic features within the passes (Table 6). Aggregations of foraging seabirds were generally not associated with stratified waters and high concentrations of chlorophyll. Rather, concentrations of seabirds were found to be associated with convergence zones in the mixed water and with the front between North Pacific water and mixed water. The mixed water in the center of the passes appeared to be the most attractive to fulmars and small alcids, while the NP/MW front was most attractive to the shearwaters. Over the two years of the study, no significant aggregations were found in either BS or NP waters.

Species that were foraging by picking at prey from the surface were associated with surface convergences that appeared to be associated with Langmuir circulation cells or tidal features (all fulmar aggregations) in the central passes (Samalga, Seguam);

whereas subsurface foraging puffins and small alcids were mostly observed in areas of turbulent, well-mixed water near the shallow regions of the passes (15 of 17 aggregations).

In contrast, short-tailed shearwater flocks that were plunge-diving for prey were associated with the front between the North Pacific and mixed waters in the passes (5/6 transects). When plunge-diving, they can dive to depths of up to 40m or more to catch prey (adult euphausiids, small forage fish) (Hunt *et al.*, 1996). Thus, prey-patches located between the surface and 40m are available to shearwaters (Vlietstra *et al.*, 2005 and references therein).

Northern fulmars forage for prey (primarily copepods) at the surface. During the Aleutian Pass surveys of 2001 and 2002, these birds were only observed in significant numbers in Seguam and Samalga passes. In contrast to shearwaters, fulmar aggregations were often spread out over the pass implying that the mechanisms concentrating their prey at the surface must be of fairly small spatial scale.

Captive tufted puffins have been shown to feed near the bottom more than other puffins and murres (Duffy *et al.*, 1987). Tufted puffins can dive up to 100 m in pursuit of prey, but most search dives are probably in the upper 60 m of the water column (Piatt and Kitaysky, 2002). They were observed in both years in all of the eastern and central passes in which we had observations with the exception of Tanaga and Amukta. Distributions of puffins were spread out and were observed over the MW region in the center of the passes with fewer distributed over the BS or NP waters.

Least auklets were observed in significant numbers only in Tanaga Pass in 2002. Auklets obtain their food by pursuit diving (Ashmole and Ashmole, 1967) and least

auklets can dive to depths of ~15 m (Obst *et al.*, 1995). Hunt *et al.* (1998) found that, in the Delarof Islands west of Tanaga Pass, thousands of least auklets congregated on the water downstream of a sill, usually between boils and sometimes around the edges of boils. These auklets were feeding primarily on copepods. Our present results suggest a similar affinity for topographically generated boils and convergences. However, least auklets also forage on near-surface patches of copepods, particularly when they are concentrated at a shallow pycnocline (Hunt *et al.*, 1990). In past cruises north of Kiska Island and northeast of Amchitka Pass, least auklets were observed foraging on near-surface patches of copepods (G.L. Hunt and K.O. Coyle unpublished observations), but in the present study, we did not have the opportunity to see if similar foraging aggregations existed over stratified water to the north of Tanaga Pass.

The interaction of strong currents with bathymetric features creates zones of vertical advection, mixing, and surface convergences that make island passes attractive foraging regions for seabirds. Deep passes lacking these features, such as Amukta Pass (Jahncke *et al.*, 2005; Ladd *et al.*, 2005) and many of the passes in the western Aleutian Archipelago, are not as likely to facilitate trophic transfer to top predators as shallow passes such as those found in the eastern Aleutian Islands. Thus, not only may there be less primary production in the central Aleutian passes (as observed in the sparse primary production data collected during 2001 and 2002; Mordy *et al.*, 2005), but the transfer of that production to higher trophic levels may be constrained by the lack of the physical processes required to create predictable regions of enhanced foraging opportunities in the deeper passes.

Most studies of seabirds in relation to physics emphasize the use of fronts or other structures that concentrate prey in the horizontal plane (Hunt *et al.*, 1999). Less frequently, there have been observations of birds using prey concentrated in the vertical plane, i.e. on the pycnocline (Hunt *et al.*, 1990). In coastal regions, marine birds forage in areas where currents interact with bathymetry to force prey toward the surface (Coyle *et al.*, 1992; Hunt *et al.*, 1998). They are also frequently found foraging in tide rips where clear frontal structures are absent (Safina and Burger, 1985; 1989; Zamon, 2003). However, within these areas of mixed water, there may be small-scale convergences forced by tidal currents that can concentrate prey. These areas are often marked by the aggregation of flotsam, or by the presence of foraging seabirds. In the present study, the presence of lines of birds foraging at the surface coincided with areas of convergence within regions of well-mixed water. These convergences were identified by accumulations of flotsam at the surface and the presence of slicks or dimpled surface waters. The present paper contributes to our understanding of seabird foraging by demonstrating the importance of physical concentrating mechanisms within areas of well-mixed water that do not fit the definition of frontal structures.

ACKNOWLEDGEMENTS

We thank the captain and crew of the R/V *Alpha Helix* for their support during this project. R.L. Pitman, L. de Souza, L.S. Vlietstra and S.W. Webb provided assistance during seabird observations. We thank A.D. Long and M.M. Riehle for modifying the RiehleTRON. J. Jahncke was supported by a Graduate Assistance in Areas of National Need (GAANN) Fellowship while working on this paper. This research was sponsored by CIFAR and NOAA's Steller Sea Lion Research Program and is contribution FOCI-L486 to Fisheries-Oceanography Coordinated Investigations and PMEL contribution number 2655. This publication was also funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA17RJ1232, Contribution #1039.

FIGURES

Figure 1. Map of eastern and central Aleutian Islands. Passes discussed in text are noted by white lines. Currents are noted by black arrows. Water depth is color coded from light blue (shallow) to dark purple (deep).

Figure 2. CTD transect through Unimak Pass on 18 June 2001 (UN0101). a) accumulated number of seabirds from the northern end of the transect, b) SST (°C) from thermosalinograph, c) surface salinity from thermosalinograph, d) surface density (kg m^{-3}), e) surface fluorescence (volts), f) CTD temperature (color scale: °C), g) CTD salinity (color scale: psu). Arrows show locations of CTD casts. White contours in bottom two plots are σ_t density (kg m^{-3}). Gray shading marks shearwater aggregation and associated physical features.

Figure 3. CTD transect through Akutan Pass on 14 June 2001 (AK0103). a) accumulated number of seabirds, b) SST (°C) from thermosalinograph, c) surface salinity from thermosalinograph, d) surface density (kg m^{-3}), e) surface fluorescence (volts), f) CTD temperature (color scale: °C), g) CTD salinity (color scale: psu). Arrows show locations of CTD casts. White contours in bottom two plots are σ_t density (kg m^{-3}). Gray shading marks shearwater aggregation and associated physical features.

Figure 4. Acoustic transect through Akutan Pass on 14 June 2001 (AK0104). a) accumulated number of seabirds, b) surface density (kg m^{-3}), c) copepod biomass (g m^{-3}), d) euphausiid biomass (g m^{-3}).

Figure 5. CTD transect through Seguam Pass on 2 June 2002 (SG0217). a) accumulated number of seabirds, b) SST (°C) from thermosalinograph, c) surface salinity from thermosalinograph, d) surface density (kg m^{-3}), e) surface fluorescence (volts), f)

CTD temperature (color scale: °C), g) CTD salinity (color scale: psu). Arrows show locations of CTD casts. White contours in bottom two plots are σ_t density (kg m^{-3}).

Figure 6. Frontal structure in Seguam Pass during two different tidal phases. a) SST and b) horizontal derivative of density during 10 June 2001 transect (SG0107) during a flood tide, c) SST and d) horizontal derivative of density during 2 June 2002 transect (SG0217) during an ebb tide.

Figure 7. Acoustic transect through Seguam Pass on 3 June 2002 (SG0218). a) accumulated number of seabirds, b) surface density (kg m^{-3}), c) copepod biomass (g m^{-3}), d) euphausiid biomass (g m^{-3}).

Figure 8. CTD transect through Tanaga Pass on 30 May 2002 (TN0220). a) accumulated number of seabirds, b) SST (°C) from thermosalinograph, c) surface salinity from thermosalinograph, d) surface density (kg m^{-3}), e) surface fluorescence (volts), f) CTD temperature (color scale: °C), g) CTD salinity (color scale: psu). Arrows show locations of CTD casts. White contours in bottom three plots are σ_t density (kg m^{-3}).

Figure 9. Schematic comparing the surface density structure and subsurface frontal structure in the eastern and central passes.

Table 1. List of all transects carried out along passes in 2001 and 2002.

Pass	Transect	Date	Survey	Start of transect				Change of tide ^a	End of transect				Distance (km)	Number of foraging seabirds			
				Time ^c	Latitude	Longitude	Tide		Time ^c	Latitude	Longitude	Tide		Shearwater	Fulmar	Puffin	Auklet ^d
					(°N)	(°W)				(°N)	(°W)						
Unimak	UN0101	18-Jun-01	CTD	06:32	54°	165°	Ebb	12:15	16:53	54°	164°	Flood	110	1,539	11	75	9
					33.45'	47.86'				08.28'	15.87'						
	UN0102	18-Jun-01	Acoustic	17:14	54°	164°	Flood	20:45 – 22:15	03:38 ^b	54°	165°	Flood	100	8	0	25	1
					08.25'	15.57'				31.30'	39.99'						
Akutan	AK0103	14-Jun-01	CTD	11:31	54°	166°	Flood	13:45	17:46	53°	165°	Ebb	50	9,510	4	60	1,182
					08.00'	26.41'				56.30'	45.07'						
	AK0104	14-Jun-01	Acoustic	19:28	53°	165°	Flood	NA	23:44	54°	166°	Flood	51	41	1	57	222
					56.28'	44.74'				08.19'	26.87'						
	AK0105	15-Jun-01	CTD	06:57	54°	166°	Ebb	08:45	14:12	53°	165°	Flood	65	5,833	17	108	52
					09.11'	30.71'				54.14'	36.74'						
Amukta	AM0106	12-Jun-01	CTD	07:06	52°	171°	Flood	10:15 – 16:45	19:31	52°	171°	Flood	65	0	7	3	6
					37.14'	50.15'				02.66'	41.94'						
Seguam	SG0107	10-Jun-01	CTD	08:07	52°	172°	Ebb	15:15	20:27	51°	172°	Flood	66	1	721	13	37
					21.05'	59.06'				54.25'	22.73'						
	SG0108	11-Jun-01	Acoustic	10:38	52°	173°	Ebb	16:15	18:39	51°	172°	Flood	70	3	934	12	23
					23.17'	02.00'				54.07'	22.52'						
0																	
Unimak	UN0201	20-May-02	Acoustic	07:44	54°	165°	Flood	13:53 – 20:44	23:46	54°	163°	Ebb	105	414	8	24	20
					31.18'	39.60'				00.29'	46.79'						

Akutan	UN0202	25-May-02	CTD	09:40	54° 33.63'	165° 48.19'	Ebb	13:42	22:26	54° 04.83'	164° 03.40'	Flood	125	15	4	58	76
	UN0203	12-Jun-02	Acoustic	06:22	54° 30.04'	165° 35.43'	Flood	07:52	15:00	54° 05.97'	164° 07.54'	Ebb	87	602	3	133	42
	UN0204	12-Jun-02	CTD	15:04	54° 05.98'	164° 07.64'	Ebb	15:40	23:05	54° 30.09'	165° 35.44'	Flood	95	120	2	184	18
	AK0205	22-May-02	CTD	07:29	54° 09.15'	166° 30.62'	Flood	15:53	18:52	53° 48.28'	165° 16.28'	Ebb	90	0	0	50	39
	AK0206	24-May-02	Acoustic	07:29	54° 09.19'	166° 30.65'	Ebb	NA	11:26	53° 58.45'	165° 52.35'	Ebb	46	0	0	16	10
	AK0207	26-May-02	Acoustic	07:21	53° 48.27'	165° 16.18'	Ebb	NA	13:32	53° 55.79'	165° 43.00'	Ebb	33	0	5	5	1
	AK0208	15-Jun-02	CTD	13:49	54° 09:25'	166° 30.59'	Ebb	16:52	22:27	53° 48.34'	165° 15.92'	Flood	90	0	2	166	23
	AK0209	16-Jun-02	Acoustic	05:00	53° 48.14'	165° 15.55'	Flood	10:33	13:25	54° 09.16'	166° 30.68'	Ebb	91	0	31	218	50
	UM0210	10-Jun-02	CTD	10:07	53° 38.13'	167° 40.88'	Ebb	14:30	15:55	53° 07.19'	167° 55.94'	Flood	65	0	0	427	136
	UM0211	10-Jun-02	Acoustic	16:28	53° 07.18'	167° 55.83'	Flood	NA	20:53	53° 33.44'	167° 39.94'	Flood	46	0	0	232	145
	SA0212	07-Jun-02	CTD	12:36	53° 05.36'	169° 16.71'	Flood	NA	16:49	52° 49.37'	169° 28.17'	Flood	32	0	450	1	0
	SA0213	08-Jun-02	CTD	09:34	52° 28.18'	169° 21.83'	Ebb	13:11	15:04	52° 49.36'	169° 28.08'	Flood	40	2	1,827	8	6
	SA0214	09-Jun-02	Acoustic	07:37	52° 28.33'	169° 21.79'	Ebb	13:51	19:29	53° 00.42'	169° 22.41'	Flood	46	0	45	6	0

Amukta	AM0215	05-Jun-02	Acoustic	11:44	52°	171°	Flood	15:15	19:58	52°	171°	Ebb	80	2	11	6	3
					02.66'	41.80'				45.26'	51.96'						
	AM0216	05-Jun-02	CTD	21:32	52°	171°	Flood	03:15	08:44 ^c	52°	171°	Ebb	65	N	N	N	N
					45.33'	52.02'				10.65'	43.64'						
Seguam	SG0217	02-Jun-02	CTD	12:29	52°	173°	Ebb	17:45	22:50	51°	172°	Flood	85	0	380	20	6
					27.73'	07.48'				52.07'	19.87'						
	SG0218	03-Jun-02	Acoustic	09:18	52°	173°	Flood	13:00	17:33	51°	172°	Ebb	85	141	3,008	53	95
					27.20'	07.44'				52.03'	19.88'						
Tanaga	TN0219	29-May-02	Acoustic	12:56	51°	177°	Ebb	14:57	22:28	52°	178°	Flood	100	0	2	8	10,417
					25.64'	44.75'				04.26'	29.08'						
	TN0220	30-May-02	CTD	09:14	52°	178°	Ebb	15:42	21:38	51°	177°	Flood	93	0	12	8	1,621
					03.97'	28.81'				26.71'	48.74'						

a = change of tide approximated from tidal charts from nearest pass with information, b = transect finished on 19-Jun-01, c = transect finished on 06-Jun-02, d = total number includes ancient murrelets, least and whiskered auklets, e = times noted in Hawaii-Aleutian Daylight Time (UTC-9), NA = not applicable, N = survey conducted at night

Table 2. Proportion of shearwaters, expected abundance (in parentheses) and 95 % confidence interval on the proportion of birds observed in each identified region along the transect. (a = Significantly greater use than expected, b = Significantly ($p < 0.05$) lower use than expected use, ns = no significant differences in use).

Pass	Transect	Seabirds counted	Distance surveyed	Location				
				Bering Sea water	BS/MW front	Mixed water	NP/MW front	North Pacific water
Unimak	UN0101	1539	106	0.01 (0.28)	<0.01 (0.06)	0.03 (0.29)	0.93 (0.15)	0.04 (0.23)
				$0.00 \leq X_i \leq 0.01$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$0.02 \leq X_i \leq 0.04$ * ^b	$0.92 \leq X_i \leq 0.95$ * ^a	$0.02 \leq X_i \leq 0.05$ * ^b
	UN0201	414	121	No identifiable physical features ¹				
	UN0203	602	97	Not encountered	Not encountered	0.38 (0.65)	0.62 (0.02)	No birds (0.33)
						$0.33 \leq X_i \leq 0.43$ * ^b	$0.57 \leq X_i \leq 0.67$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b
Akutan	UN0204	120	97	Not encountered	Not encountered	0.51 (0.64)	0.49 (0.11)	No birds (0.25)
						$0.40 \leq X_i \leq 0.63$ * ^b	$0.37 \leq X_i \leq 0.6$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b
	AK0103	9510	39	No birds (0.14)	No birds (0.09)	<0.01 (0.55)	1.00 (0.10)	<0.01 (0.11)
				$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$1.00 \leq X_i \leq 1.00$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b
	AK0105	5833	61	No birds (0.07)	No birds (0.07)	0.34 (0.56)	0.63 (0.06)	0.03 (0.25)
Seguam				$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$0.32 \leq X_i \leq 0.35$ * ^b	$0.62 \leq X_i \leq 0.65$ * ^a	$0.02 \leq X_i \leq 0.03$ * ^b
	SG0218	141	84	0.29 (0.40)	0.09 (0.03)	0.62 (0.37)	No birds (0.05)	No birds (0.16)
				$0.19 \leq X_i \leq 0.39$ * ^b	$0.02 \leq X_i \leq 0.15$ ns	$0.52 \leq X_i \leq 0.73$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b

¹ Significantly high densities of shearwaters at the northern end of the transect near 54.5° N, not associated with an evident front.

Table 3. Proportion of ancient murrelets (ANMU), least auklets (LEAU) and whiskered auklets (WHAU) expected abundance (in parentheses) and 95 % confidence interval on the proportion of birds observed in each identified region along the transect. (a = Significantly greater use than expected, b = Significantly ($p < 0.05$) lower use than expected use, ns = no significant differences in use).

Pass	Transect	Species	Seabirds counted	Distance surveyed	Location				
					Bering Sea water	BS/MW front	Mixed water	NP/MW front	North Pacific water
Unimak	UN0202	ANMU	76	126	No birds (0.30)	No identifiable	0.71 (0.46)	No identifiable	0.29 (0.25)
					$0.00 \leq X_i \leq 0.00$ * ^b	frontal region	$0.58 \leq X_i \leq 0.84$ * ^a	frontal region	$0.16 \leq X_i \leq 0.42$ ^{ns}
Akutan	AK0103	ANMU	72	39	No birds (0.14)	No birds (0.09)	1.00 (0.55)	No birds (0.10)	No birds (0.11)
					$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$1.00 \leq X_i \leq 1.00$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b
	AK0103	WHAU	1110	39	No birds (0.14)	No birds (0.09)	1.00 (0.55)	No birds (0.10)	No birds (0.11)
					$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$1.00 \leq X_i \leq 1.00$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b
	AK0104	WHAU	206	35	Not encountered	Not encountered	0.82 (0.73)	0.18 (0.12)	No birds (0.15)
							$0.75 \leq X_i \leq 0.89$ * ^a	$0.11 \leq X_i \leq 0.25$ ^{ns}	$0.00 \leq X_i \leq 0.00$ * ^b
Umnak	UM0210	ANMU	134	62	No identifiable physical features ¹				
	UM0211	ANMU	143	57	No identifiable physical features ²				
Tanaga	TN0219	LEAU	10384	101	0.11 (0.49)	<0.01 (0.02)	0.89 (0.27)	No birds (0.02)	No birds (0.20)
					$0.10 \leq X_i \leq 0.11$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$0.89 \leq X_i \leq 0.90$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b
	TN0220	LEAU	1593	93	0.10 (0.46)	0.03 (0.06)	0.88 (0.21)	<0.01 (0.17)	No birds (0.09)
					$0.08 \leq X_i \leq 0.12$ * ^b	$0.02 \leq X_i \leq 0.04$ * ^b	$0.85 \leq X_i \leq 0.90$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b

¹ Significantly high densities of ancient murrelets found at the central region of transect in the vicinity of 53.5° N, not associated with evident feature.

² Significantly high densities of ancient murrelets found at the northern and central regions of transect in the vicinity of 53.5 and 53.4° N, likely associated with convergence areas.

Table 4. Proportion of tufted puffins, expected abundance (in parentheses) and 95 % confidence interval on the proportion of birds observed in each identified region along the transect. (a = Significantly greater use than expected, b = Significantly ($p < 0.05$) lower use than expected use, ns = no significant differences in use).

Pass	Transect	Seabirds counted	Distance surveyed	Location				
				Bering Sea water	BS/MW front	Mixed water	NP/MW front	North Pacific water
Unimak	UN0101	75	106	0.07 (0.28)	No birds (0.06)	No birds (0.29)	0.71 (0.15)	0.23 (0.23)
				$0.00 \leq X_i \leq 0.14$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b	$0.57 \leq X_i \leq 0.84$ * ^a	$0.10 \leq X_i \leq 0.35$ ^{ns}
	UN0202	58	126	No birds (0.30)	No identifiable	0.72 (0.46)	No identifiable	0.28 (0.25)
				$0.00 \leq X_i \leq 0.00$ * ^b	frontal region	$0.57 \leq X_i \leq 0.87$ * ^a	frontal region	$0.13 \leq X_i \leq 0.43$ ^{ns}
	UN0203	133	97	Not encountered	Not encountered	0.76 (0.65)	0.08 (0.02)	0.16 (0.33)
						$0.66 \leq X_i \leq 0.85$ * ^a	$0.02 \leq X_i \leq 0.14$ ^{ns}	$0.08 \leq X_i \leq 0.24$ * ^b
	UN0204	184	97	Not encountered	Not encountered	0.84 (0.64)	0.13 (0.11)	0.03 (0.25)
						$0.77 \leq X_i \leq 0.91$ * ^a	$0.07 \leq X_i \leq 0.19$ ^{ns}	$0.00 \leq X_i \leq 0.07$ * ^b
Akutan	AK0103	60	39	0.02 (0.14)	0.05 (0.09)	0.75 (0.55)	0.08 (0.10)	0.10 (0.11)
				$0.00 \leq X_i \leq 0.06$ * ^b	$0.00 \leq X_i \leq 0.12$ ^{ns}	$0.61 \leq X_i \leq 0.89$ * ^a	$0.00 \leq X_i \leq 0.18$ ^{ns}	$0.00 \leq X_i \leq 0.20$ ^{ns}
	AK0104	57	35	Not encountered	Not encountered	0.81 (0.73)	0.09 (0.12)	0.11 (0.15)
						$0.67 \leq X_i \leq 0.94$ ^{ns}	$-0.01 \leq X_i \leq 0.18$ ^{ns}	$0 \leq X_i \leq 0.21$ ^{ns}
	AK0105	108	61	0.01 (0.07)	0.02 (0.07)	0.94 (0.56)	0.03 (0.06)	0.01 (0.25)
				$0.00 \leq X_i \leq 0.03$ * ^b	$0.00 \leq X_i \leq 0.05$ * ^b	$0.87 \leq X_i \leq 1.00$ * ^a	$0.00 \leq X_i \leq 0.07$ ^{ns}	$0.00 \leq X_i \leq 0.03$ * ^b
	AK0205	50	90	Not encountered	Not encountered	0.96 (0.59)	No birds (0.04)	0.04 (0.37)
						$0.89 \leq X_i \leq 1.03$ * ^a	$0.00 \leq X_i \leq 0.00$ * ^b	$0.00 \leq X_i \leq 0.11$ * ^b
	AK0208	165	89	0.10 (0.15)	0.18 (0.04)	0.69 (0.44)	No birds (0.06)	0.03 (0.30)

				$0.04 \leq X_i \leq 0.16$ ^{ns}	$0.10 \leq X_i \leq 0.25$ ^{*a}	$0.60 \leq X_i \leq 0.79$ ^{*a}	$0.00 \leq X_i \leq 0.00$ ^{*b}	$0.00 \leq X_i \leq 0.06$ ^{*b}
	AK0209	218	70	Not encountered	Not encountered	1.00 (0.84)	No birds (0.07)	No birds (0.09)
						$1.00 \leq X_i \leq 1.00$ ^{*a}	$0.00 \leq X_i \leq 0.00$ ^{*b}	$0.00 \leq X_i \leq 0.00$ ^{*b}
Umnak	UM0210	427	62	_____	No identifiable physical features ¹ _____			
	UM0211	232	57	_____	No identifiable physical features ² _____			
Seguam	SG0218	53	84	0.23 (0.40)	0.04 (0.03)	0.68 (0.37)	0.02 (0.05)	0.04 (0.16)
				$0.08 \leq X_i \leq 0.37$ ^{*b}	$0.00 \leq X_i \leq 0.11$ ^{ns}	$0.51 \leq X_i \leq 0.84$ ^{*a}	$0.00 \leq X_i \leq 0.07$ ^{ns}	$0.00 \leq X_i \leq 0.11$ ^{*b}

1 Significantly high densities of puffins in the central region of transect in the vicinity of 53.3° N, foraging over a strong tide rip area.

2 Significantly high densities of puffins found in the northern region of transect north of 53.4° N, likely associated with convergence areas.

Table 5. Proportion of northern fulmars, expected abundance (in parentheses) and 95 % confidence interval on the proportion of birds observed in each identified region along the transect. (a = Significantly greater use than expected, b = Significantly ($p < 0.05$) lower use than expected use, ns = no significant differences in use).

Pass	Transect	Seabirds counted	Distance surveyed	Location				
				Bering Sea water	BS/MW front	Mixed water	NP/MW front	North Pacific water
Samalga	SA0212	450	41	No identifiable physical features ¹				
	SA0213	1827	43	No identifiable physical features ²				
Seguam	SG0107	721	98	0.01 (0.10)	0.06 (0.08)	0.88 (0.43)	0.03 (0.03)	0.01 (0.35)
				$0.00 \leq X_i \leq 0.02$ * ^b	$0.04 \leq X_i \leq 0.08$ * ^b	$0.85 \leq X_i \leq 0.91$ * ^a	$0.02 \leq X_i \leq 0.05$ ^{ns}	$0.00 \leq X_i \leq 0.02$ * ^b
	SG0108	934	70	0.04 (0.34)	0.28 (0.30)	0.54 (0.17)	0.08 (0.03)	0.06 (0.16)
				$0.02 \leq X_i \leq 0.05$ * ^b	$0.25 \leq X_i \leq 0.32$ ^{ns}	$0.50 \leq X_i \leq 0.58$ * ^a	$0.06 \leq X_i \leq 0.10$ * ^a	$0.04 \leq X_i \leq 0.08$ * ^b
	SG0217	380	67	0.01 (0.42)	0.24 (0.03)	0.74 (0.50)	0.02 (0.05)	Not encountered
				$0.00 \leq X_i \leq 0.02$ * ^b	$0.18 \leq X_i \leq 0.29$ * ^a	$0.68 \leq X_i \leq 0.79$ * ^a	$0.00 \leq X_i \leq 0.03$ * ^b	
	SG0218	3008	84	0.30 (0.40)	0.08 (0.03)	0.62 (0.37)	<0.01 (0.05)	<0.01 (0.16)
				$0.28 \leq X_i \leq 0.32$ * ^b	$0.07 \leq X_i \leq 0.09$ * ^a	$0.6 \leq X_i \leq 0.64$ * ^a	$0.00 \leq X_i \leq 0.01$ * ^b	$0.00 \leq X_i \leq 0.00$ * ^b

¹ Significantly high densities of fulmars between the northern and central regions of transect near 52.9° N, fulmars were lined up on Langmuir cells.

² Significantly high densities of fulmars at central region of transect in the vicinity of 52.8° N, fulmars were foraging in tight flocks over water slicks.

Table 6. Summary of hydrographic features at which significant concentrations of seabirds occurred in Aleutian Passes. Data are ratios of significant aggregations to number of encounters with the hydrographic feature in passes where a species was present.

	Bering Sea	BS/MW		NP/MW	North Pacific
	Water	Front	Mixed Water	Front	Water
Northern					
Fulmar	0/4	2/4	4/4	1/4	0/3
Short-tailed					
Shearwater	0/4	0/4	1/6	5/6	0/6
Small Alcids	0/5	0/4	6/6	0/5	0/6
Tufted Puffin	0/6	1/5	9/11	1/10	0/11

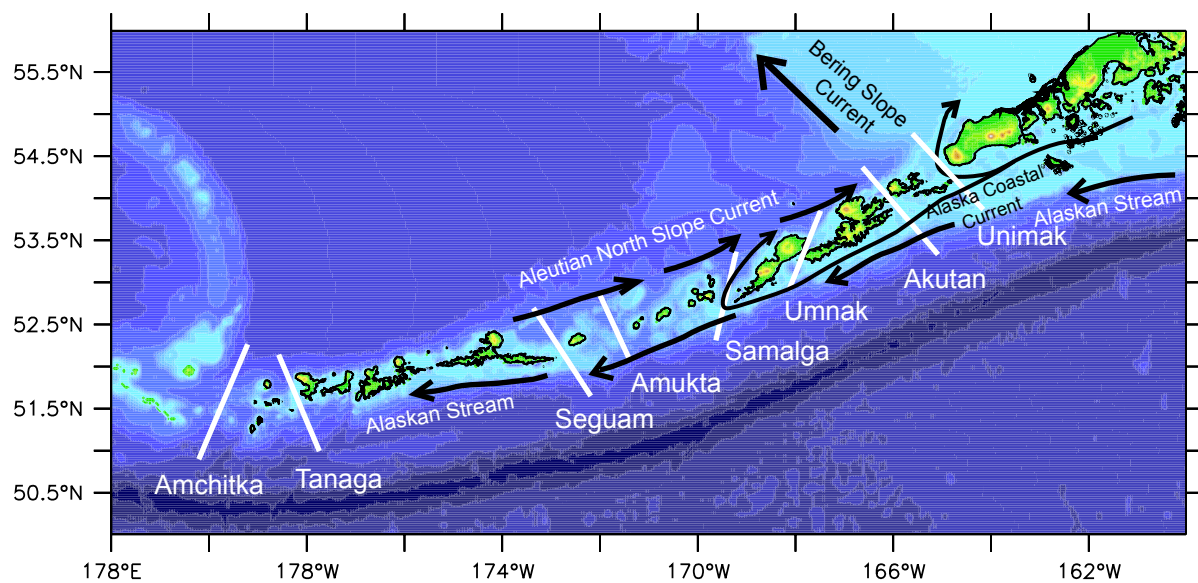
REFERENCES

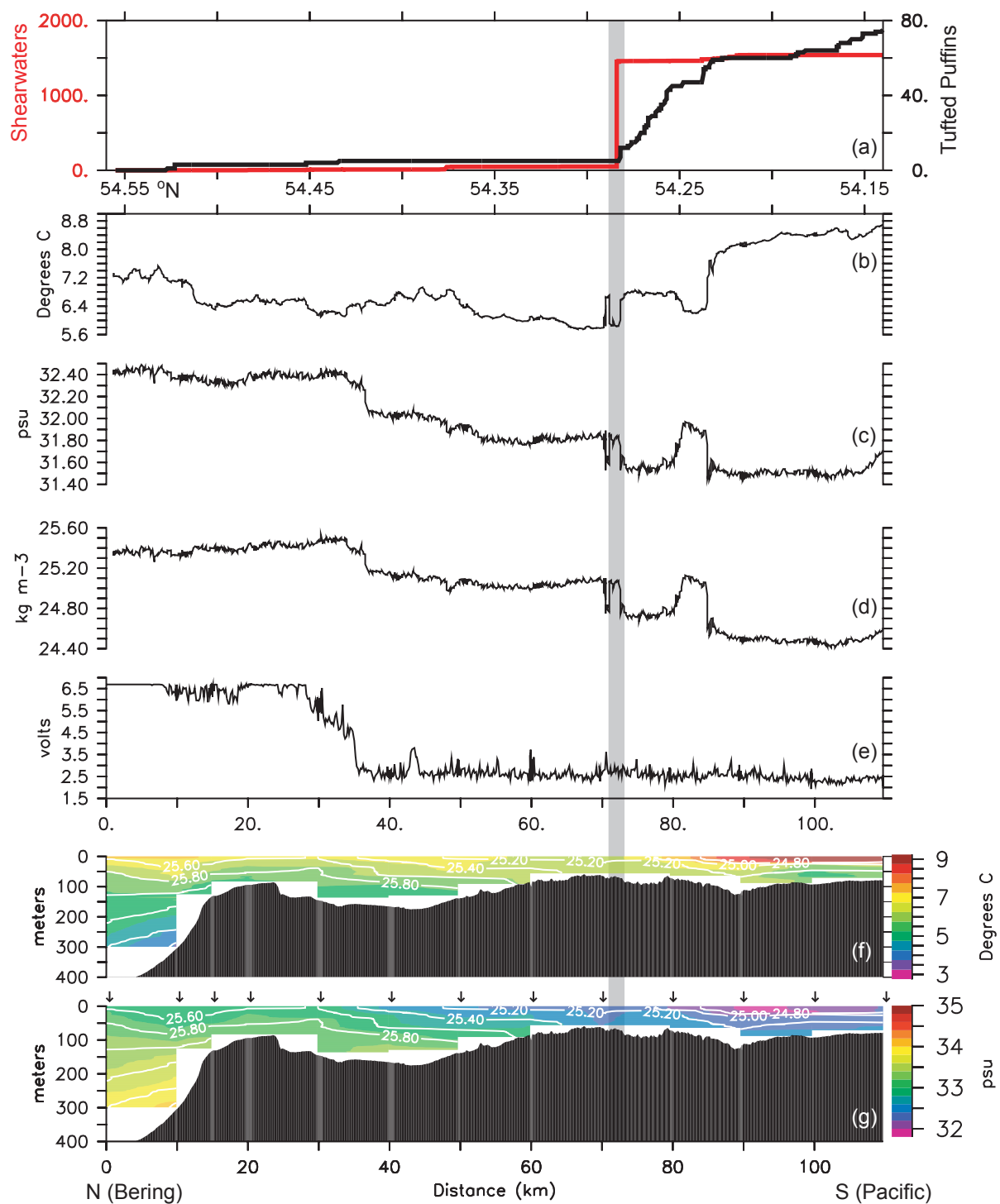
- Ashmole, N.P. and Ashmole, M.J. (1967) Comparative feeding ecology of seabirds of a tropical oceanic island. *Bull. Peabody Mus. Nat. Hist.* **24**:1-131.
- Cooney, R.T. (1989) Acoustic evidence for the vertical partitioning of biomass in the epipelagic zone of the Gulf of Alaska. *Deep Sea Res.* **36**:1177-1189.
- Coyle, K.O. (2005) Zooplankton distribution, abundance and biomass relative to water masses in eastern and central Aleutian Island passes. *Fish. Oceanogr.* this issue.
- Coyle, K.O., Hunt, G.L., Jr., Decker, M.B., and Weingartner, T. (1992) Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. *Mar. Ecol. Prog. Ser.* **83**:1-14.
- Duffy, D.C., Todd, F.S., and Siegfried, W.R. (1987) Submarine foraging behavior of alcids in an artificial environment. *Zoo Biology* **6**:373-378.
- Fragopoulou, N. and Lykakis, J. (1990) Vertical distribution and nocturnal migration of zooplankton in relation to the development of the seasonal thermocline in Patraikos Gulf. *Marine biology* **104**:381-387.
- Franks, P.J.S. (1992) Sink or swim - Accumulation of biomass at fronts. *Mar. Ecol. Prog. Ser.* **82**:1-12.
- Genin, A., Haury, L., and Greenblatt, P. (1988) Interactions of migrating zooplankton with shallow topography: Predation by rockfishes and intensification of patchiness. *Deep Sea Res.* **35**:151-175.
- Haney, J.C. and Solow, A.R. (1992) Testing for resource use and selection by marine birds. *Journal of Field Ornithology* **63**:43-52.

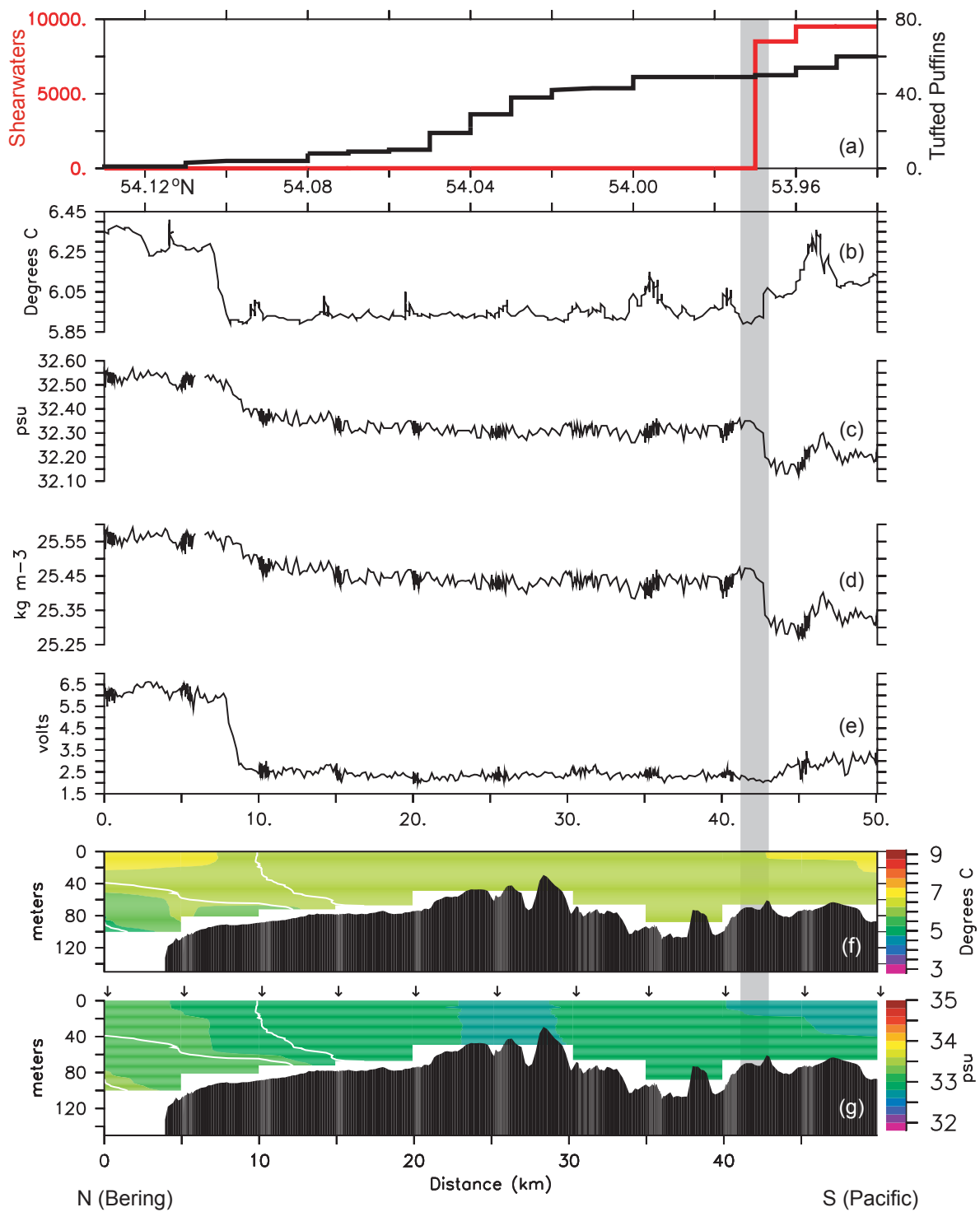
- Hunt, G.L., Jr., Harrison, N.M., and Cooney, R.T. (1990) The influence of hydrographic structure and prey abundance on foraging of least auklets. *Studies in Avian Biology* **14**:7-22.
- Hunt, G.L., Jr., Russell, R.W., Coyle, K.O., and Weingartner, T. (1998) Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Mar. Ecol. Prog. Ser.* **167**:241-259.
- Hunt, G.L., Jr., Coyle, K.O., Hoffman, S., Decker, M.B., and Flint, E.N. (1996) Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. *Mar. Ecol. Prog. Ser.* **141**:1-11.
- Hunt, G.L., Jr., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B., and Becker, P.H. (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: *Proc. 22 Int. Ornithol. Congr., Durban.*, N. J. Adams and R. H. Slotow, (eds), Johannesburg: BirdLife South Africa, pp. 2040-2056.
- Jahncke, J., Coyle, K.O., and Hunt, G.L., Jr. (2005) Seabird distribution, abundance and diets in the central and eastern Aleutian Islands. *Fish. Oceanogr.* this issue.
- Ladd, C., Hunt, G.L., Jr., Mordy, C.W., Salo, S.A., and Stabeno, P.J. (2005) Marine environment of the eastern and central Aleutian Islands. *Fish. Oceanogr.* this issue.
- Mordy, C.W., Stabeno, P.J., Ladd, C., Zeeman, S.I., Wisegarver, D.P., and Hunt Jr., G.L. (2005) Nutrients and primary production along the eastern Aleutian Island Archipelago. *Fish. Oceanogr.* this issue.
- Neu, C.W., Byers, C.R., and Peek, J.M. (1974) A technique for analysis of utilization-availability data. *J. Wildl. Manage.* **38**:541-545.

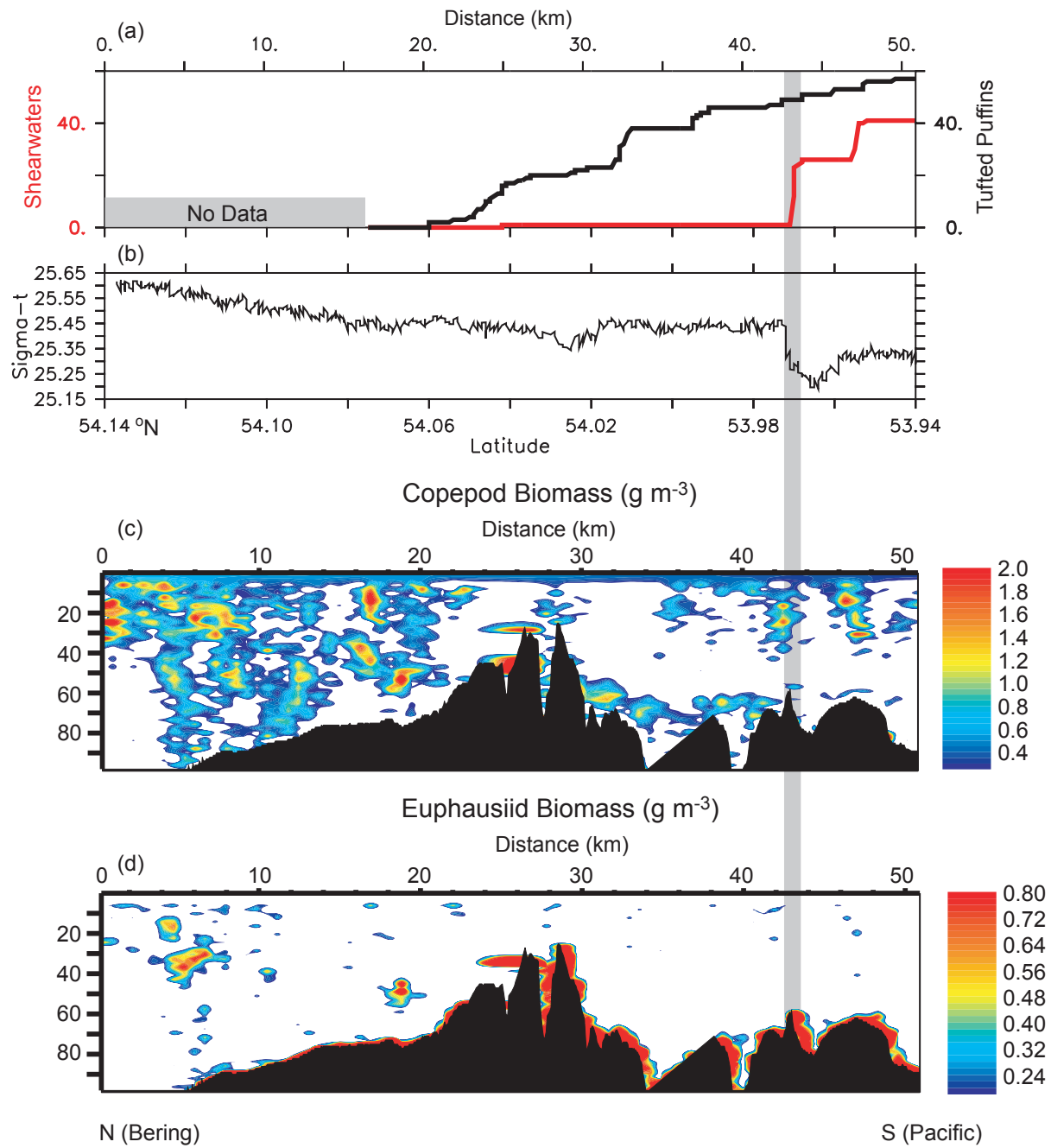
- Obst, B.S., Russell, R.W., Hunt, G.L., Jr., Eppley, Z.A., and Harrison, N.M. (1995) Foraging radii and energetics of Least Auklets (*Aethia-Pusilla*) breeding on 3 Bering Sea Islands. *Physiological Zoology* **68**:647-672.
- Piatt, J.F. and Kitaysky, A.S. (2002) Tufted Puffin (*Fratercula cirrhata*). In: *The Birds of North America*, No. 708, A. Poole and F. Gill, (eds), Philadelphia, pp. 1-31.
- Riehle, M.M., Bennett, A.F., and Long, A.D. (2001) Genetic architecture of thermal adaptation in *Escherichia coli*. *Proceedings of the National Academy of Sciences of the United States of America* **98**:525-530.
- Safina, C. and Burger, J. (1985) Common Tern Foraging - Seasonal Trends in Prey Fish Densities and Competition with Bluefish. *Ecology* **66**:1457-1463.
- Safina, C. and Burger, J. (1989) Ecological dynamics among prey fish, bluefish, and foraging Common Terns in an Atlantic coastal system. In: *Seabirds and other marine vertebrates*, J. Burger, (ed.) New York: Columbia University Press, pp. 95-173.
- Simard, Y., de Ladurantaye, R., and Therriault, J.-C. (1986) Aggregation of euphausiids along a coastal shelf in an upwelling environment. *Mar. Ecol. Prog. Ser.* **32**:203-215.
- Stabeno, P.J., Kachel, D.G., Kachel, N.B., and Sullivan, M.E. (2005) Observations from moorings in the Aleutian Passes: temperature, salinity and transport. *Fish. Oceanogr.* this issue.
- Tasker, M.L., Jones, P.H., Dixon, T., and Blake, B.F. (1984) Counting seabirds at sea from ships - a review of methods employed and a suggestion for a standardized approach. *Auk* **101**:567-577.

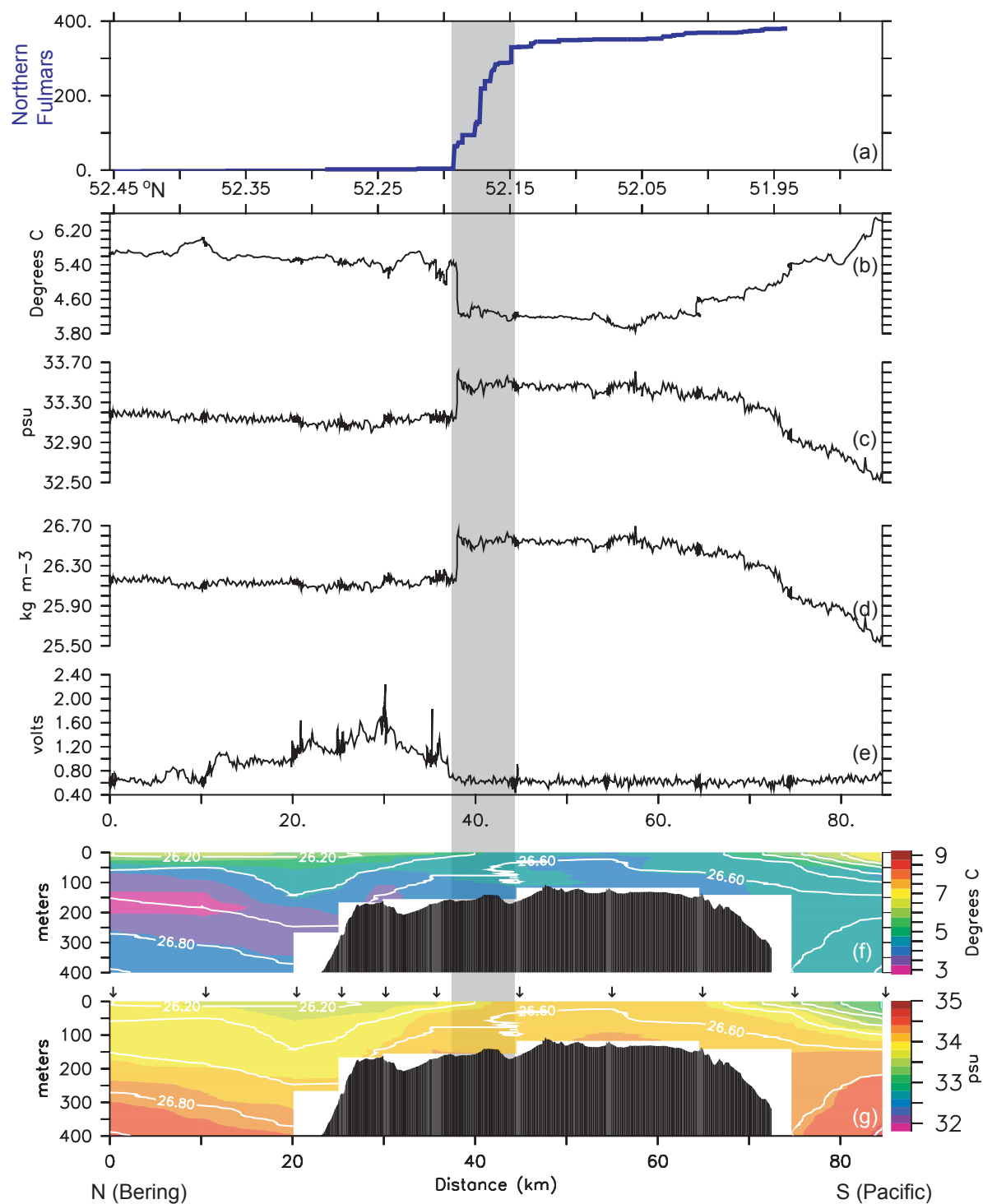
- Vlietstra, L.S., Coyle, K.O., Kachel, N.B., and Hunt, G.L., Jr. (2005) Tidal front affects prey-size use by a top marine predator. *Fish. Oceanogr.* this issue.
- Wolanski, E. and Hamner, W. (1988) Topographically controlled fronts in the ocean and their biological influence. *Science* **241**:177-181.
- Zamon, J.E. (2003) Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Mar. Ecol. Prog. Ser.* **261**:243-255.

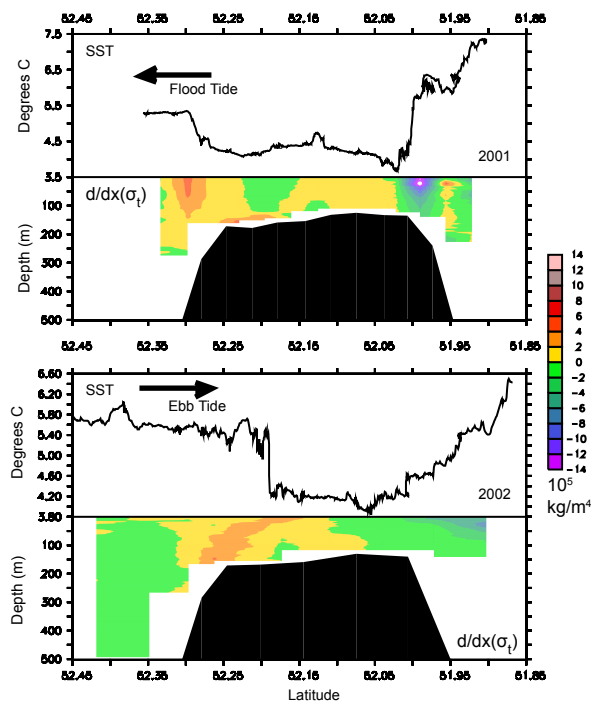


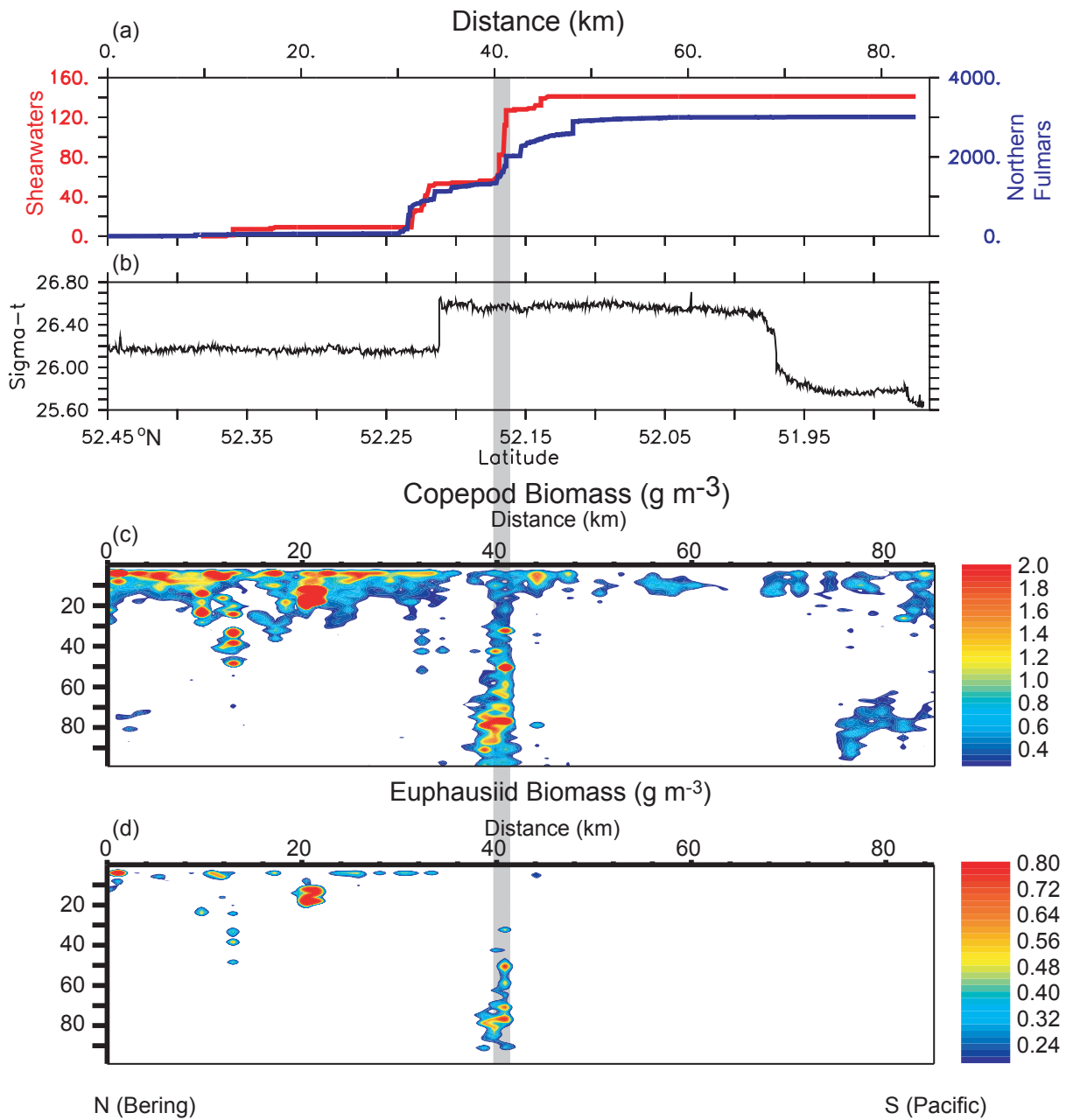


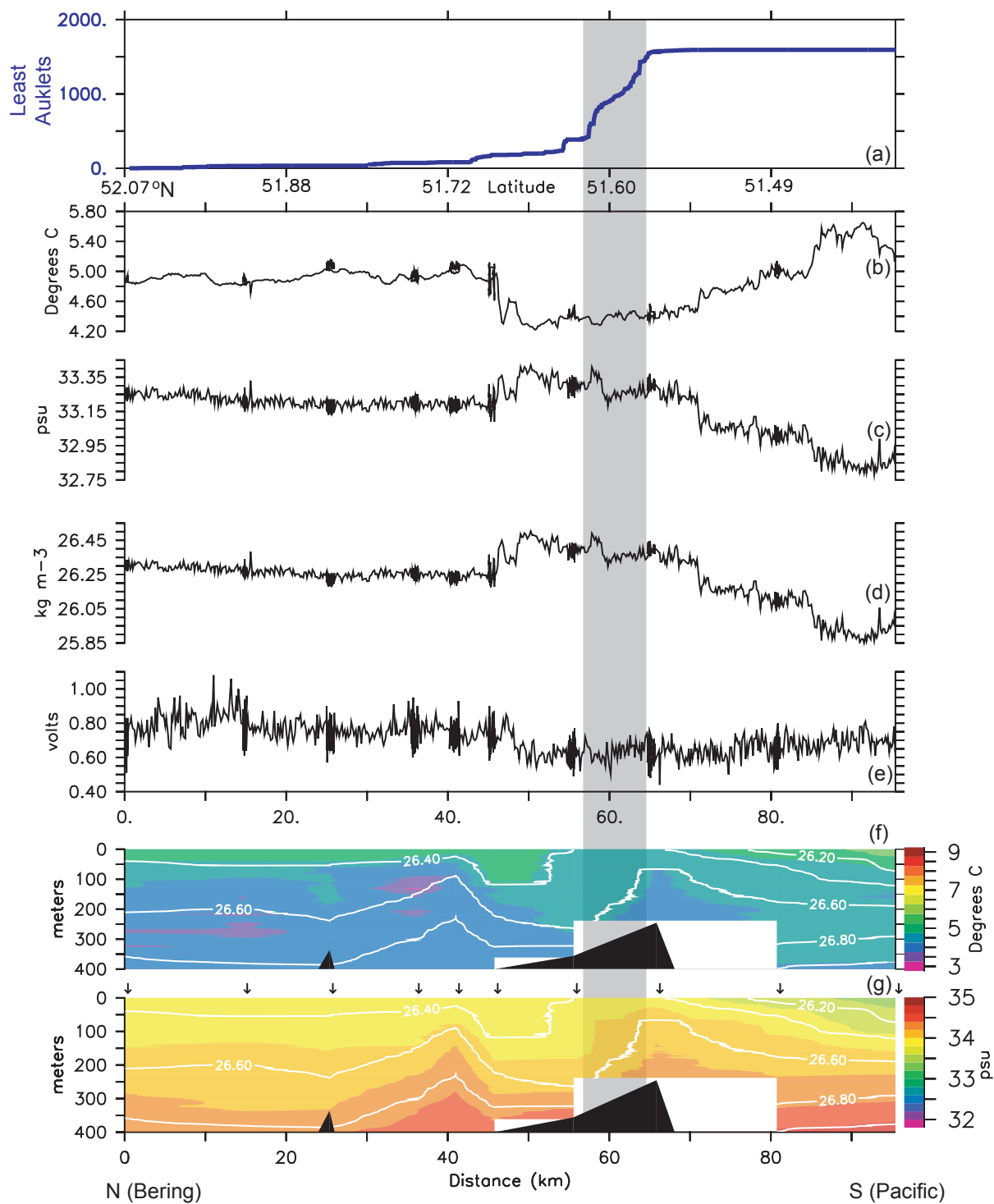




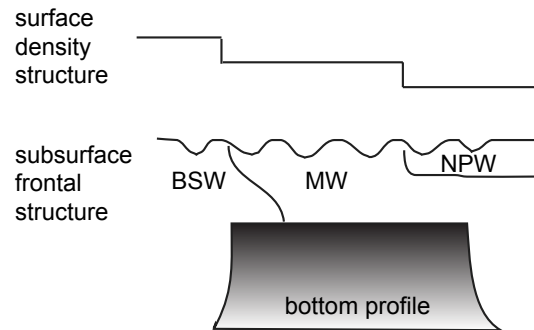








Eastern Passes (Unimak, Akutan):



Central Passes (Seguam, Tanaga):

